

THE EFFECT OF CLIMATIC VARIABILITY ON GROWTH,  
REPRODUCTION, AND POPULATION VIABILITY OF A SENSITIVE  
SALT MARSH PLANT SPECIES,  
*LASTHENIA GLABRATA* SUBSP. *COULTERI* (ASTERACEAE)

LORRAINE S. PARSONS<sup>1</sup> AND ADAM W. WHELCHER<sup>2,3</sup>

<sup>1</sup>Point Reyes National Seashore, Point Reyes Station, CA 94956

<sup>2</sup>URS Corp., Box 290, 201 Willowbrook Blvd., Wayne, NJ 07474

ABSTRACT

As with many other sensitive species in California, the range of *Lasthenia glabrata* Lindley subsp. *coulteri* (A. Gray) Ornd. (Asteraceae; Coulter's goldfields) has been dramatically reduced in recent decades by urbanization. Many populations are small, isolated, and seemingly unstable. In this study, we conducted an autecological assessment of a small *L. glabrata* subsp. *coulteri* population at San Diego County's San Dieguito Lagoon, using a large population at San Elijo Lagoon for comparison. The large population was not only more stable based on trends in seed production, but generally produced larger plants and more flowers and capitulescences than the small population. However, this relationship appears to be temporally variable and influenced significantly by climatic conditions, particularly rainfall totals and distribution. In a year with above-average rainfall, vegetative and reproductive yield of plants in the small population (San Dieguito Lagoon) matched or even exceeded that of plants in the large one (San Elijo Lagoon), which was subjected to prolonged inundation following heavy rains and a back-up of run-off and creek flows behind a dike system. Rainfall is linked not only to soil moisture, but to nutrient influx and cycling, variables that were strongly associated with group (marsh/monitoring year) separation and prediction in statistical analyses. When resources are sufficient, reproductive yield appears to be driven by other factors, the most probable of which is pollen supply. The relationship between rainfall and plant yield could prove integral to predicting long-term viability of *L. glabrata* subsp. *coulteri* populations, as above-average rainfall years are often sporadic and interspersed between lengthy periods of average or below-average rainfall in southern California. Conservation and enhancement of the remaining coastal salt marsh *L. glabrata* subsp. *coulteri* populations could perhaps be furthered by factoring this relationship into conservation and restoration projects and hydrologic regimes designed for managed wetland systems.

Small populations of rare plant species face many genetic, demographic, and ecological challenges. Small populations can suffer from reduced "fitness," often undergoing one or more genetic bottleneck events that reduce genetic variation (Nei et al. 1975; Hamrick et al. 1979; Hedrick 1983; Ledig 1986; Barrett and Kohn 1991 and others). Fewer numbers also create a greater chance for normally outbreeding species to inbreed and become less fit through concentration of deleterious alleles (Charlesworth and Charlesworth 1987 and others). Opportunities for gene flow between populations—and the potential for infusion of new alleles—may be minimal due to the dwindling number of populations and the distance between them. Small plant populations are intrinsically less appealing to pollinators (Powell and Powell 1987; Morgan 1999), which can further reduce fecundity and the potential for even limited outbreeding between more distant individuals. Reduced genetic variation can also increase small populations' susceptibility to herbivory, pathogens, and stochastic factors such as floods and environmental and demographic variability (Shaffer 1981). In addition, population viability can be continually jeopardized by human-related disturbances or changes in wa-

tershed or ecosystem conditions—sometimes the very changes believed to have made the species rare in the place. Even efforts to better manage, enhance, or restore systems in which rare plants occur can pose a threat if these activities do not balance their ecological requirements with those of other target plant and wildlife species and the ecosystem as a whole.

Determining whether small populations are succumbing to these challenges is not an easy task. Annual censuses are not only difficult, but often misleading unless conducted over several decades due to cryptic life history stages (i.e., seed banks) and normal fluctuations in population size that may have little impact on population stability or viability (Davy and Jefferies 1981; Schemske et al. 1994; Pavlik 1994 and others). A life table or population viability analysis (PVA) is often considered the optimal approach for assessing population stability (Schemske et al. 1994; Pavlik 1994; Menges 1986). However, the probability of a long-lived seed bank immeasurably complicates performance of a life table or PVA for plant species (Pavlik 1994), despite arguments that there are ways to circumvent calculation of this unknown (Menges 1986). Some alternative approaches to assessing population stabil-

ity involve performance of non-integrated demographic trend assessment, which focuses on overall trajectories in survivorship, seed production, density of viable seed, and frequency of establishment (Pavlik 1994). Morphological attributes associated with productivity or yield such as plant size/biomass and flower number may be incorporated, as well (Menges 1986; Menges and Gordon 1996). These analyses are often improved through using either wetter congeners or large, more stable populations of the same species for comparison (Pavlik 1994).

Consistent with the major role that extrinsic disturbances or changes can play in population viability, many studies on rare species include an ecological, as well as demographic, component (Schemske et al. 1994). Some have criticized researchers for emphasizing autecology over demography in sensitive plant research, characterizing ecological research as premature in the absence of demographic information relevant to population vital rates (Schemske et al. 1994). However, managers of reserves and enhancement/restoration projects often seek ecological information that might help them better manage reserves or design projects (Pavlik 1994). Moreover, ecological data can greatly complement demographic assessments, particularly when the information is integrated to allow for identification of ecological constraints on key life history stages and variables associated with productivity (e.g., plant size, flower number) (Schemske et al. 1994; Pavlik 1994; Menges and Gordon 1996).

San Dieguito Lagoon in San Diego County supports a small population of a rare plant, *Lasthenia glabrata* Lindley subsp. *coulteri* (A. Gray) Ornd. (Asteraceae: Coulter's goldfields). For a sensitive species, *L. glabrata* subsp. *coulteri* has a remarkably diverse distribution. This annual is found in alkali playas in southern California's arid inland areas and salt marshes and vernal pools in the region's more moderate coastal areas (NDDb 1998; Skinner and Pavlik 1994; Hickman 1993).

This diverse distribution has not spared the species from the threat of extirpation, however. All of these habitats have been negatively impacted to some extent by California's extensive urbanization over the past 50 y (Skinner and Pavlik 1994). More than 90 percent of California's wetland habitats, including marshes, vernal pools, and alkali playas, have been destroyed by commercial and residential development, and despite regulatory efforts at effecting a "no net loss" policy, this downward trend in wetland habitat acreage appears to be continuing. The wetland habitats that remain are often fragmented, highly disturbed, and heavily impacted by outside influences such as nutrient and contaminant influx associated with watershed development. The toll these habitat losses and impacts has taken is apparent from the constriction of the species' his-

toric range. In recent decades, its once extensive distribution throughout southern California has been reduced to a few marshes and vernal pools in San Diego, Ventura, and Santa Barbara counties and alkali playas in Riverside County (NDDb 1998).

This precipitous decline in distribution prompted listing of *L. glabrata* subsp. *coulteri* as a species of concern (formerly C2) by the U.S. Fish and Wildlife Service and a species of limited distribution (List 1B) by the California Native Plant Society (CNPS). While its cousin, *Lasthenia glabrata* Lindley subsp. *glabrata*, is relatively common and has even a larger range than subsp. *coulteri*, other *Lasthenia* species that occur in vernal pool habitats such as *Lasthenia burkei* (E. Greene) E. Greene (Burke's goldfields) and *Lasthenia conjugens* E. Greene (Contra Costa goldfields) are faced with similar threats in terms of potential extirpation (Skinner and Pavlik 1994). Within its historic coastal range, *L. glabrata* subsp. *coulteri* often grows in high elevation areas of salt marshes—or the "high marsh"—alongside another sensitive species, *Cordylanthus maritimus* Benth. subsp. *maritimus* (salt marsh bird's beak), a state- and federally listed endangered species.

San Dieguito Lagoon is one of six San Diego County coastal marsh systems that supports historical and/or possibly reintroduced populations of *L. glabrata* subsp. *coulteri*. The species was once present at 10 San Diego County marshes (NDDb 1998), but probably in low abundance, as an early ecological study characterized it as only an "infrequent" inhabitant (Purser 1942). Of the six remaining occurrences, three are believed to be small and relatively unstable populations, including the one at San Dieguito Lagoon. Over the past few decades, *L. glabrata* subsp. *coulteri* numbers at San Dieguito Lagoon have ranged from as low as zero in 1980 (Sea Science Services and Pacific Southwest Biological Services, Inc. 1980) and six in 2000 (Andrea Thorpe personal communication) to as high as 1000 individuals during the mid- and late-1990s (MEC Analytical, Inc. 1993; L. Parsons and A. Whelchel, personal observation). Neighboring marshes such as San Elijo Lagoon, as well as reportedly Los Peñasquitos Lagoon, support annual populations consistently numbering as many as 5000 to 10,000 individuals (L. Parsons and A. Whelchel personal observation).

San Dieguito Lagoon is also one of seven coastal marshes in San Diego County, CA, for which restoration and/or enhancement activities have been or are being conducted or are proposed. As with other San Diego County marshes, this coastal lagoon has been subject to a number of historic watershed changes and disturbances, including damming of its river, agricultural and residential development, diking, and intermittent mouth closures that impound water and create hypoxic conditions. With restora-

tion and enhancement plans for San Dieguito Lagoon currently being developed, there appeared to be a strong and immediate need for information on demographic and ecological aspects of this small and possibly unstable population and its potential for conservation and even future enhancement. Few studies have actually assessed demography or autecological relationships of this or other *Lasthenia* species. The research that exists deals primarily with upland species (*Lasthenia californica* Lindley; Rajakaruna and Bohm 1999; Vivrette 1999) or focuses on salinity tolerance (*L. glabrata* subsp. *coulteri*; Kingsbury et al. 1976; Callaway et al. 1990; Callaway and Sabraw 1994).

In 1996, a study was implemented to assess demographic and ecological characteristics of the *L. glabrata* subsp. *coulteri* population at San Dieguito Lagoon. For purposes of performing a comparative assessment, we broadened the scope of our study to include another *L. glabrata* subsp. *coulteri* population that appeared to be larger and more stable in terms of plant numbers, the population at San Elijo Lagoon, located directly north of San Dieguito Lagoon. Through this study, we hoped to gain insight into differences in survivorship, reproductive potential (plant size, flower number) and success (seed set and seed production) between populations. When possible, we also attempted to track trends in demographic results for purposes of assessing population stability. By comparing autecology of a small and unstable population with that of a large and stable one, we hoped to increase our understanding of the biotic and abiotic factors that might be influencing variations in plant yield and population viability. We believe that this information could prove invaluable to resource managers charged with planning or implementing complex restoration or conservation projects, particularly projects with multiple species and ecosystem objectives.

**Study area.** San Dieguito Lagoon is located in Del Mar, CA, approximately 25 km north of San Diego (Fig. 1). The lagoon's principal source of freshwater is the San Dieguito River, which has been dammed to create Lake Hodges, a reservoir in the inland area of the San Diego County. Watershed of the lagoon totals 897 km<sup>2</sup>, 785.2 km<sup>2</sup> of which is behind dams (California Wetlands Information System 1996). During the summer and fall, the lagoon mouth sometimes closes for several weeks to a month until it re-opens either naturally or manually (i.e., using bulldozers). Vegetation communities occurring within the lagoon include salt and brackish marshes and, at its eastern end, freshwater marsh and limited riparian habitats. Approximately 104 of the 240 hectares of wetlands once present at San Dieguito Lagoon still remain (California Wetlands Information System 1996). In addition to damming, the watershed of the lagoon has been altered considerably by development of

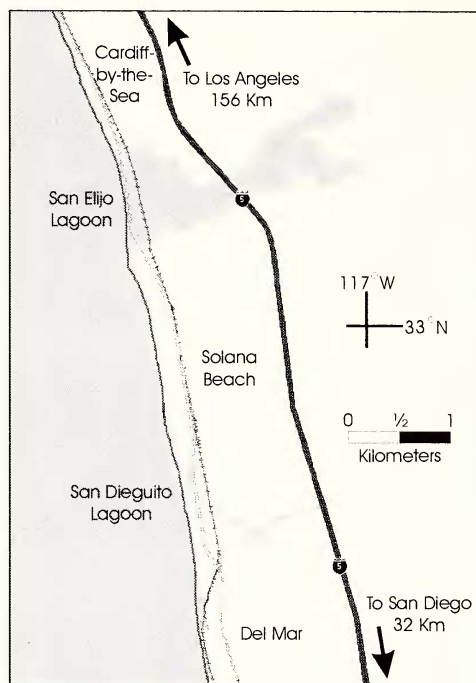


FIG. 1. Location of *Lasthenia glabrata* subsp. *coulteri* (Coulter's goldfields) study areas in San Diego County, CA.

the adjacent floodplain and uplands for agriculture, commercial and residential structures, and a race-track/fairgrounds. The population of *L. glabrata* subsp. *coulteri* at this lagoon is located in a muted tidal basin in the southern portion of the lagoon, approximately 2 km from the mouth.

San Elijo Lagoon is located in the Cardiff, CA, approximately 27.5 km north of San Diego and directly north of San Dieguito Lagoon (Fig. 1). Several creeks flow into the lagoon, one of which is dammed by Lake Wohlford (Escondido Creek). The watershed for San Elijo Lagoon is 200.2 km<sup>2</sup> (California Wetlands Information System 1996). The mouth of San Elijo Lagoon also closes during the summer and fall, typically with more frequency and longer duration than San Dieguito Lagoon. Current wetland acreage at San Elijo Lagoon totals 230.4 ha and is comprised of salt marsh, brackish marsh, freshwater marsh, and riparian habitat (California Wetlands Information System 1996). The watershed of this lagoon has been altered considerably by development of the adjacent floodplain and uplands for farming and commercial and residential structures. The lagoon has also been separated into a series of hydrologic "cells" by construction of a series of dikes and levees between 1880 and 1940. By closing flood gates at one of the eastern dikes, the area east of Interstate 5 is partially flooded from November through March for waterfowl enhancement (Susan Welker personal communication). The population of *L. glabrata* subsp.



TABLE 1. MEAN ANNUAL TEMPERATURE AND RAINFALL AND NUMBER OF DAYS THAT LAGOON MOUTH WAS OPEN DURING THE STUDY PERIOD (1996–1999).

Year end	San Diego NWS-Lindbergh (NOAA; CDWR)				San Dieguito Lagoon		San Elijo Lagoon	
	Temperature (Jan–Dec)	Departure from mean	Rainfall (Oct–April)	Departure from mean	No. of days mouth open*	% of year	No. of days mouth open**	% of year
	mean (deg.C)	(% of mean)	total (cm)	(% of mean total)				
1996	17.8	99.4	12.85	53.4	351	96	80	22
1997	18	100.5	17.48	72.7	358	98	153	42
1998	18.5	103.4	42.75	177.8	338	92	238	65
1999	15.6	87.2	16.2	67.4	219***	60	240	66

NOAA = National Oceanic Atmospheric Administration Center, National Climatic Data Center

CDWR = California Department of Water Resources, California Data Exchange Center, CIMIS

\* = H. Elwany, unpublished data; San Diego County Department of Environmental Health

\*\* = San Diego County Parks Department, unpublished data

\*\*\* = All closure events occurred after April 1999 and plant senescence

*coulteri* at this lagoon occurs at the eastern end of the lagoon in an area that receives little to no direct tidal flow, although some subsurface tidal inflow may occur.

Mean annual temperature and rainfall data and data for the number of days the lagoon mouths were open for the study period (1996–1999) are provided in Table 1. Rainfall was 53 to 73 percent of average during October–April in 1996, 1997, and 1999 and 178 percent of average during those months in 1998. Annual mean daily temperature showed less variation (87 to 103 percent of average between 1996–1999).

METHODS

Annual Monitoring

*Demography.* In general, demographic information was collected in 1996, 1997, 1998, and 1999 at San Dieguito Lagoon and in 1997, 1998, and 1999 at San Elijo Lagoon. To assess demography, 14 plants within each of 10 sampling locations (0.5 × 0.5 m plots) were haphazardly chosen and marked in late January or early February of each monitoring year, when the plants were 1 to 2 cm tall seedlings. The sampling locations were chosen as representative of the microhabitat diversity and environmental heterogeneity present with the populations' existing range at each marsh. Mortality and phenology were assessed on a monthly or twice monthly basis for three months: February, March, and April. Mortality was assessed as the number of marked plants that died between marking and mid-April. Phenology was broken into three basic stages: vegetative, in bud, and flowering. In addition, plants were examined for signs of potential herbivory. In mid-April, when most plants had already set seed, a minimum of 10 plants and a maximum of 14 plants were harvested from each sampling location to determine aboveground plant height (cm), number of capitulescences (inflorescences), capitulescence diameter (the diameter of

the receptacle in mm excluding ray flowers), number of flowers (total of disc and ray flowers), number of seeds, and seed set (number of seeds/number of flowers). Seeds were also examined for signs of granivory or seed predation.

There were some exceptions to the described demographic monitoring. Mortality was not assessed during the following marsh/years—San Dieguito Lagoon 1996 and 1999 and San Elijo Lagoon 1999—but plants were harvested in mid-April for measurement of plant height, capitulescence number and diameter, flower and seed number, and seed set. Efforts were made to assess survivorship at San Dieguito Lagoon and San Elijo Lagoon in 1998, but a sedimentation event associated with higher-than-average water levels in the study area at San Elijo Lagoon caused marking materials (colored rubberbands) to be obscured. The 1998 data for San Dieguito Lagoon was incomplete, as information on mortality was not collected in April.

*Biotic variables.* Density of *L. glabrata* subsp. *coulteri* was assessed biweekly in 1997 using a 0.5 × 0.5 m quadrat subdivided into 25 1-dm<sup>2</sup> subquadrats. One of the subquadrats was randomly chosen, and the number of *L. glabrata* subsp. *coulteri* individuals present within the subquadrat was counted. Also, vegetative cover within the sampling plot was assessed one time per monitoring year using the 36 cross points of the subdivided 0.5 × 0.5 m quadrat and recording the species or bareground occurring below the cross point. For analysis purposes, percent cover was calculated for *L. glabrata* subsp. *coulteri*, total vegetation cover, and cover of non-native species. Total vegetation cover included both native and non-native species. Native species were primarily coastal salt marsh inhabitants such as *Salicornia virginica* L. (pickleweed), *Salicornia subterminalis* Parish (glasswort), *Frankenia salina* (Molina) I. M. Johnston (alkali heath), *Cressa truxillensis* Kunth (alkali weed), and *Spergularia marina* (L.) Grisels. (sand-spurrey). Non-native spe-



cies included *Cotula coronopifolia* L. (brass-butons), *Mesembryanthemum crystallinum* L. (crystalline iceplant), *Lolium multiflorum* Lam. (Italian ryegrass), *Parapholis incurva* (L.) C. E. Hubb. (sickle grass), *Polypogon monspeliensis* (L.) Desf. (annual beard grass), and *Poa annua* L. (annual bluegrass).

**Abiotic variables.** A total of 11 abiotic variables was assessed during each monitoring year, except 1999. The abiotic variables were soil pH, soil salinity, soil moisture, organic matter, ammonium, nitrates + nitrites, phosphorous, cation exchange capacity (CEC), calcium, magnesium, and potassium. Soil texture was assessed at both marshes in 1997. As this species grows in high marsh areas, which are only infrequently inundated, reduction-oxidation potential was not measured. Soil pH, soil salinity, and soil moisture was measured twice a month (1997) to monthly (1998) from 15-cm-deep soil core samples at all 10 sampling locations. Soil pH was measured by creating soil pastes in the field and measuring with an Oakton pHTestr 3 ( $\pm 0.01$  pH resolution) field pH probe. Soil salinity was measured by expressing soil water from a syringe fitted with filter paper onto a refractometer, which reports salinities in grams per kilogram. Soil moisture was measured by removing 10- to 15-cm soil cores and assessing loss of mass on drying (Gardner 1986). For nutrient analysis, five of the 10 sampling locations at each marsh were randomly selected for subsampling twice each monitoring year (mid-February and mid-March). At these subsampling locations, approximately 100 g of soil was removed, air dried, and sent to A&L Western Agricultural Laboratories (Modesto, California) for measurement of organic matter, ammonium, nitrates + nitrites, phosphorous, cation exchange capacity, calcium, magnesium, and potassium. In 1997, the laboratory also analyzed soil texture. The procedures described above were performed for both marshes during the years monitoring was performed, with the exception of San Dieguito Lagoon in 1996 and 1999 and San Elijo Lagoon in 1999. Soil salinity was not measured at San Dieguito Lagoon in 1996, and pH, soil moisture, organic matter, and other nutrients were only analyzed once during the 1996 monitoring year. Data for variables sampled more than once per season were averaged for analysis.

**Data analysis.** Differences in plant population dynamics between marshes and sampling years were assessed by treating each "marsh/year" sampled independently and conducting a One-Way Analysis of Variance using the Systat computing package (SPSS, Chicago, IL). For the density comparison, a t-test was conducted to test for differences in plant density between marshes. When assumptions for parametric tests were not met, data were either transformed, or an equivalent, non-parametric procedure (e.g., Kruskal-Wallis) was

conducted. If a significant difference was found, differences between particular means were analyzed further by using either Tukey, T'-method (Sokal and Rohlf 1981), or non-parametric Tukey-type (Zar 1984) multiple comparison procedures. The dependent variable plant height was log-transformed for analysis.

Discriminant function analysis was used to explore the association between plant population dynamics and 13 biotic and abiotic factors within marshes. Quadratic discriminant function analyses were performed, because they are less sensitive to dissimilarities in covariance matrices between groups. Groupings used in analyses were based on results from the Analysis of Variance tests, with generally low yield plots separated from high yield plots. The analyses incorporated data from 1996–1998: no biotic and abiotic data were collected in 1999. As salinity data were not available for San Dieguito in 1996, a preliminary analysis was performed using models that incorporated the salinity variable, but not the San Dieguito 1996 data. If salinity did not have a strong loading on any canonical variable, a second or final analysis was performed using models that incorporate San Dieguito 1996 data, but not the salinity variable. For the reproductive success analyses in which groups were smaller, fewer than 13 variables were incorporated, using F-to-enter from the preliminary analyses as the criterion. Discriminant function analyses were conducted using the Systat computing package. The following variables were log transformed for analysis: ammonium, nitrate + nitrite, calcium, and cation exchange capacity.

## RESULTS

**Comparison of plant yield between marshes.** One of the intents of our study was to compare attributes of a small, and perhaps unstable, population with those of a large and stable one. A component of this study involved assessment of demographic variables associated with survivorship and yield to determine the degree to which these populations actually differ other than in estimated population size. As shown in Figure 2, there were statistically significant differences between marsh/years for mean survivorship (per 0.25 m<sup>2</sup> plot; ANOVA,  $F = 8.67$ ,  $n = 30$ ,  $P = 0.001$ ), mean plant height (ANOVA,  $F = 56.8$ ,  $n = 69$ ,  $P < 0.001$ ), mean capitulescence number (Kruskal-Wallis, Test Stat. = 46.3,  $n = 69$ ,  $P < 0.001$ ), mean capitulescence diameter (ANOVA,  $F = 19.6$ ,  $n = 69$ ,  $P < 0.001$ ), mean flower number (Kruskal-Wallis, Test Stat. = 28.5,  $n = 49$ ,  $P < 0.001$ ), mean number of seeds produced (seed number) (Kruskal-Wallis, Test Stat. = 54.3,  $n = 69$ ,  $P = 0.001$ ), and mean seed set (mean number of seeds/mean number of flowers) (ANOVA,  $F = 25.1$ ,  $n = 49$ ,  $P < 0.001$ ). The mean percent cover of *L. glabrata* subsp. *coulteri* within 0.25m<sup>2</sup> sampling plots also differed between marsh/years

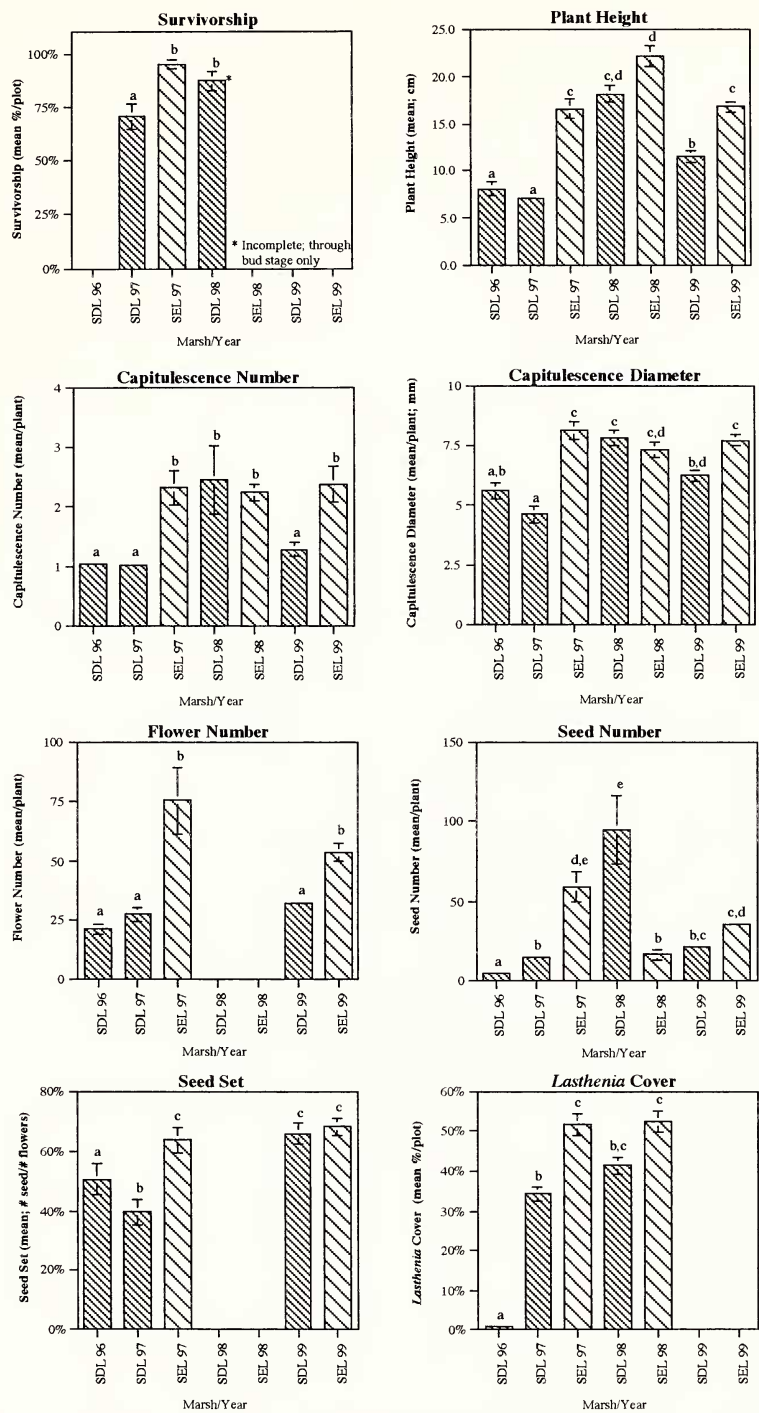


FIG. 2. Means for dependent plant variables in marsh/years studied. Differences between marsh/years were significant for all analyses (P for all ANOVA/Kruskal-Wallis = or < 0.001). Differences between particular means are indicated by small case letters. Bars represent plus or minus 1 SE (standard error): means seemingly without bars are ones with very small standard errors. Plot refers to individual sampling plots, which were 0.25 m<sup>2</sup> in size.

(Kruskal-Wallis, Test Stat. = 26.12,  $n = 49$ ,  $P < 0.001$ ). Measurements of these variables were not assessed for all marsh/years. Specifically, survivorship data were only available for three marsh/years, and survivorship for San Dieguito Lagoon 1998 was assessed only through bud stage. Data for mean flower number, mean seed set, and cover of *L. glabrata* subsp. *coulteri* were only available for five marsh/years.

Closer examination of the results and multiple comparison tests reveals some interesting trends. Survivorship through the vegetative stage was lower at San Dieguito Lagoon 1997 than at San Elijo Lagoon 1997 and San Dieguito Lagoon 1998 (Fig. 2). However, despite these statistical differences, seedling survivorship at both marshes remained generally high (>70 percent). Based on biweekly censuses for marked individuals, most mortality occurred just prior to or after reproduction. In 1997, total survivorship at reproductive maturity (flowering stage) was 72 percent for San Dieguito Lagoon and 95 percent for San Elijo Lagoon. As the San Dieguito Lagoon population matured more quickly than San Elijo Lagoon, it is probable that some of the mortality occurred after reproduction and therefore actually constituted senescence. The results suggest that, at least in 1997, the populations were following the Deevey Type 1 survivorship curve characteristic of stable populations (Pavlik 1994), in that the mortality inflection point followed onset of seed production. Furthermore, as the data for San Dieguito 1997 was recorded during a below-average rainfall year, low mortality cannot necessarily be ascribed to above-average environmental conditions.

Means for plant height, capitulescence diameter and number, and flower number also showed some interesting relationships. Means were not only generally lower at San Dieguito Lagoon than at San Elijo Lagoon, but remarkably similar between years within the respective marshes. There was one exception. In 1998, yield of the San Dieguito Lagoon plants was actually closer to that of the 1997, 1998, and 1999 San Elijo Lagoon plants. Means for plant height and capitulescence diameter suggested that San Dieguito Lagoon 1999 might be intermediate between low and high yield marsh/years, but those for capitulescence and flower number were equivalent to means in low yield years.

Results for seed set and seed number were somewhat more complex. Plants at San Dieguito Lagoon set less seed in 1997 than in 1996, and seed set (number of seeds/number of flowers) was lower in both of these marsh/years than in San Dieguito Lagoon 1999 and San Elijo Lagoon 1997 and 1999. For the total number of seeds produced, however, the 1996 San Dieguito Lagoon marsh/year was the least productive. The distinction between the remaining marsh/years was less clearcut, but in terms of seed productivity, the ranking appeared to be, from lowest to highest, as follows: San Dieguito

Lagoon 1997 and San Elijo Lagoon 1998; San Dieguito Lagoon 1999; San Elijo Lagoon 1999; San Elijo Lagoon 1997; and San Dieguito Lagoon 1998. Unlike the 1997 survivorship data, these results suggest that the San Dieguito Lagoon population might be less stable than that of the larger San Elijo Lagoon one. Based on non-integrated demographic trend analysis, seed production per individual of stable populations should consistently equal or exceed that of a common congener or more stable population (Pavlik 1994). With the exception of 1998, seed production of the San Dieguito Lagoon plants was typically lower than those at San Elijo Lagoon. The large differences observed in annual population size may have only exacerbated this disparity in seed production between populations.

*Plant yield and influence of biotic and abiotic factors.* The dissimilar patterns in sample means observed for mean seed number and seed set and the other plant variables may relate to an underlying difference in how biotic and abiotic factors affect various stages or aspects of plant development. Based on these patterns, we decided to analyze our results by dividing our results into two grouping structures—reproductive potential and reproductive success. Reproductive potential measures the potential of the plant to be more reproductively successful through survivorship to reproduction (mortality), being larger (mean plant height), and producing more capitulescences (mean capitulescence number) and more flowers (mean capitulescence diameter and mean flower number). All of these variables relate to an individual's ability to outcompete another in terms of attracting pollinators or utilizing limited resources (e.g., water, nitrogen, etc.). Reproductive success measures the actual success of an individual in reproducing, as determined by seed number and seed set (percentage of flowers producing seed).

For dependent variables such as plant height, capitulescence diameter and number, and flower number, marsh/years generally split into two groups based on yield, with San Dieguito Lagoon 1996, 1997, and 1999 in a low yield group (Reproductive Potential 1/RP1) and San Dieguito Lagoon 1998 and San Elijo Lagoon 1997, 1998, and 1999 in a high yield group (Reproductive Potential 2). For the dependent variables seed number and seed set, groupings were less distinct, but marsh/years were separated into three groups, with San Dieguito Lagoon 1996 in a low yield group (Reproductive Success 1/RS1), San Dieguito Lagoon 1997 and San Elijo Lagoon 1998 in an intermediate yield group (Reproductive Success 2/RS2), and San Elijo Lagoon 1997 and 1999 and San Dieguito Lagoon 1998 and 1999 in a high yield group (Reproductive Success 3/RS3).

Reproductive potential of a germinated seedling is typically affected by herbivory, environmental factors, and intra- and inter-specific competition.



Herbivory can negatively affect individuals through consumption of either vegetative tissue or flowers, which may weaken or kill the plant. Through the three years of study, no herbivory of vegetative tissue or flowers was observed at either marsh. The effect of intra- and inter-specific competition is not as directly observable and can be more complicated. At high intra- or inter-specific densities, seedlings can compete for resources or light or become more attractive to herbivores. At later stages, however, high densities of synchronously flowering individuals, including non-native neighbors such as *Cotula coronopifolia*, may also serve to attract pollinators and thereby enhance reproductive success.

Some estimates of *L. glabrata* subsp. *coulteri* density were collected in 1997, and densities ranged from three individuals (San Elijo Lagoon) to 140 individuals (San Dieguito Lagoon) per dm<sup>2</sup>. Overall, the 1997 sampling plots at San Dieguito Lagoon had higher densities per dm<sup>2</sup> ( $71.6 \pm \text{SE } 13.5$ ) than those at San Elijo Lagoon ( $28.4 \pm \text{SE } 7.2$ ) (*t*-test,  $t = 2.83$ ,  $n = 20$ ,  $P = 0.011$ ). Densities of other species were not estimated, but cover of other native species ranged from 0 to 75 percent, and cover of non-native species ranged from 0 to 50 percent. Extremely low total mortality rates for vegetative and flowering individuals at both marshes in 1997 (~72 to 95 percent) suggests that either abundance of *L. glabrata* subsp. *coulteri* or other species was not high enough, or resources not limited enough, to have induced either intra- and inter-specific competition at the seedling or vegetative stage during this year. While above-average rainfall may have increased seedling densities at San Dieguito Lagoon in 1998, the fact that 89 percent of the plants reached at least bud stage suggests that densities were not high enough to incur density-dependent mortality.

Reproductive success is affected by all the same factors as reproductive potential, but other factors can limit reproduction, as well, specifically granivory (herbivory of unfertilized ovules or seed) and, for non-vegetative species such as *L. glabrata* subsp. *coulteri*, pollination success. Based on statistical analyses, reproductive success was highest for the RS3 group (San Elijo Lagoon 1997 and 1999 and San Dieguito Lagoon 1998 and 1999) and lowest in the RS1 group (San Dieguito Lagoon 1996). The fact that marsh/years with technically equivalent reproductive potential (San Dieguito Lagoon 1996 and 1998) should have differing rates of reproductive success suggests that a different factor or suite of factors may be affecting seed number and seed set.

As noted earlier, no consumption of entire flowers was observed during the three years of study, and low mortality rates indicate that most individuals survived to flowering and seed set. It is possible that competition among individuals for resources increased during the flowering stage, as ambient temperatures and rates of evaporation and evapotrans-

piration typically climb during the warm spring months. Flowering often coincides with a neap tide series, a period of extremely low tides that often decrease soil moisture and increase evaporation rates and soil salinity in higher marsh elevations.

Some granivory was actually observed in seeds of San Dieguito Lagoon individuals in 1998. The extent of granivory was not quantified, but in general, the number of individuals and/or number of seeds per individual that appeared to have been affected was relatively low. While viability of the damaged seeds was not tested, the damage appeared extensive enough to render the seeds inviable. Granivory, or pre-dispersal predation, was not observed in the other study years at this marsh, nor was it observed in seeds of plants from San Elijo Lagoon. The presence of organisms that would remove seeds after dispersal, including ground-dwelling insects such as ants, was sporadic, and even when present, abundance was low. Ground-dwelling organisms observed within *L. glabrata* subsp. *coulteri* patches included ants (Formicidae), thrips (Thysanoptera), and rove (Staphylinidae) and other beetles (*Bembidion* sp. and Dermestidae) (Wesley Maffei personal communication). With the exception of ants, these invertebrates are considered unlikely post-dispersal seed predators. None of these organisms, including the ants, were observed removing fallen seeds, nor were birds observed foraging in these areas.

Pollination was not included within the scope of our study, but many insects were observed visiting flowers during our sampling efforts. The primary insect visitors appeared to be solitary bees (*Andrena pallidifovea* and *A. cercocarpi*), beetles (Dermestidae, *Geocoris* sp.), beeflies (Bombyliidae), flies (*Bufo lucilia* sp. and *Nemotelus* sp.), butterflies (*Coenonympha californica*), and halictine or "sweat" bees (*Lasioglossum* sp.) (W. Maffei personal communication; Robbin Thorp personal communication). Several of these visitors have the potential to effect pollination either through collecting pollen (e.g., Andrenidae or halictine bees) or foraging on pollen or other flower parts (e.g., Dermestidae). Overall, visitor numbers and species diversity appeared to be lower at San Dieguito Lagoon than at San Elijo Lagoon, although no formal pollinator observations were conducted.

Based on these observations, we hypothesize that resources such as nutrients and perhaps even pollen may be the primary determinants or reproductive potential and success.

*Discriminant function analysis.* To explore further the association between biotic and abiotic factors and the groupings of marsh/years suggested by results of multiple comparison testing, discriminant function analyses were performed. The question posed by these analyses was two-fold. Using the groups suggested by multiple comparison testing, was there some combination of biotic and abiotic

TABLE 2. RESULTS OF THE DISCRIMINANT FUNCTION ANALYSES FOR THE REPRODUCTIVE POTENTIAL AND SUCCESS MODELS.

Reproductive Potential Model

Canonical Variable: 0.002\*pH - 0.193\*organicmatter - 1.330\*soilmoisture + 1.092\*phosphorous - 0.005\*potassium - 0.189\*magnesium - 0.443\*totalplantcover - 0.406\*ammonium\_log - 0.113\*nitrates + nitrites\_log + 0.326\*non-nativeplantcover - 0.487\*calcium\_log - 0.699\*CEC\_log

Classification results: Actual groups	Results—Cases (%)		Jackknifed Results—Cases (%)	
	RP1	RP2	RP1	RP2
RP1	16(100)	0	15(94)	1(6)
RP2	0	15(100)	0	15(100)
Total % Correct		100		97

Reproductive Success Model

Canonical Variable 1: 0.386\*pH - 1.235\*soilmoisture - 0.651\*organicmatter + 0.937\*phosphorous - 0.438\*potassium + 0.106\*magnesium + 0.422\*totalplantcover + 0.756\*ammonium\_log + 1.406\*nitrates + nitrites\_log

Canonical Variable 2: 0.482\*pH + 0.771\*soilmoisture + 0.258\*organicmatter - 1.265\*phosphorous + 0.421\*potassium + 0.786\*magnesium + 0.253\*totalplantcover + 0.754\*ammonium\_log + 0.497\*nitrates + nitrites\_log

Classification results: Actual groups	Results—Cases (%)			Jackknifed Results—Cases (%)		
	RS1 (%)	RS2 (%)	RS3 (%)	RS1 (%)	RS2 (%)	RS3 (%)
RS1	10(100)	0	0	10(100)	0	0
RS2	0	11(100)	0	0	11(100)	0
RS3	0	0	10(100)	0	0	10(100)
Total % Correct			100			100

Group Means for Models

Variables measured	Reproductive Potential		Reproductive Success		
	RP1	RP2	RS1	RS2	RS3
pH	7.59	7.83	7.43	7.78	7.90
% Soil moisture	29.6	40.3	25.9	37.2	41
% Organic matter	2.62	3.65	1.84	3.39	4.11
Phosphorous (ppm)	46.1	52.7	39.90	53.41	54.05
Potassium (ppm)	414.6	346.6	425.60	347.86	375.10
Magnesium (ppm)	1036.6	1104.2	1024.60	1030.82	1156.35
% Total plant cover	76.3	64	89.8	65.9	55.7
Log-Ammonium (ppm)	1.15	1.11	1.09	1.09	1.22
Log-Nitrates + Nitrites (ppm)	1.38	1.06	1.68	0.96	1.06
% Non-native plant cover	27	8.5	25.0NI	19.2NI	9.9NI
Log-Calcium (ppm)	3.42	3.76	3.35NI	3.65NI	3.75NI
Log-CEC (meq/100g)	1.75	2.26	1.83NI	2.12NI	2.04NI
Soil salinity (ppt)	58.7NI	33.1NI	NA	38.6NI	42.4NI

NA-Not available; NI-Not included in models (see Methods and/or Results for explanation.)

variables that would allow us to discriminate between these groups? And, if so, what combination of variables would allow us to best predict the group to which the sampling location belonged? Two models were used. One model separated sampling locations into two groups (RP1, RP2) based on differences in sample means for reproductive potential variables, and another separated sampling locations into three groups (RS1, RS2, and RS3) based on differences in sample means for reproductive success variables. The groupings were essentially the same as described previously, except for the absence of San Dieguito Lagoon and San Elijo Lagoon 1999: no biotic and abiotic data were collected in 1999. The 13 biotic and abiotic variables used in the models were: pH, salinity, soil moisture, organic matter, ammonium, nitrates + nitrites, phosphorous, potassium, magnesium, calcium, cation exchange capacity, total vegetation cover, and non-native plant species cover. While soil salinity appeared to be higher for RP1 than RP2 (Table 2), it did not have a strong loading in preliminary analyses for either model or correlation with other variables and was therefore not incorporated into final analyses.

According to the reproductive potential analysis, the biotic and abiotic variables used discriminated well between the groups suggested by multiple comparison results ( $F = 8.34$ ,  $n = 31$ ,  $P < 0.0001$ ). Canonical scores of group means were 2.21 for RP1 and -2.36 for RP2. The canonical discriminant function accounted for approximately 100 percent of the total dispersion in the data. Based on the standardized functions, most of the group separation came from soil moisture, phosphorous, calcium, and cation exchange capacity. The canonical variable and a list of group means is provided in Table 2. Using the canonical variable, the model

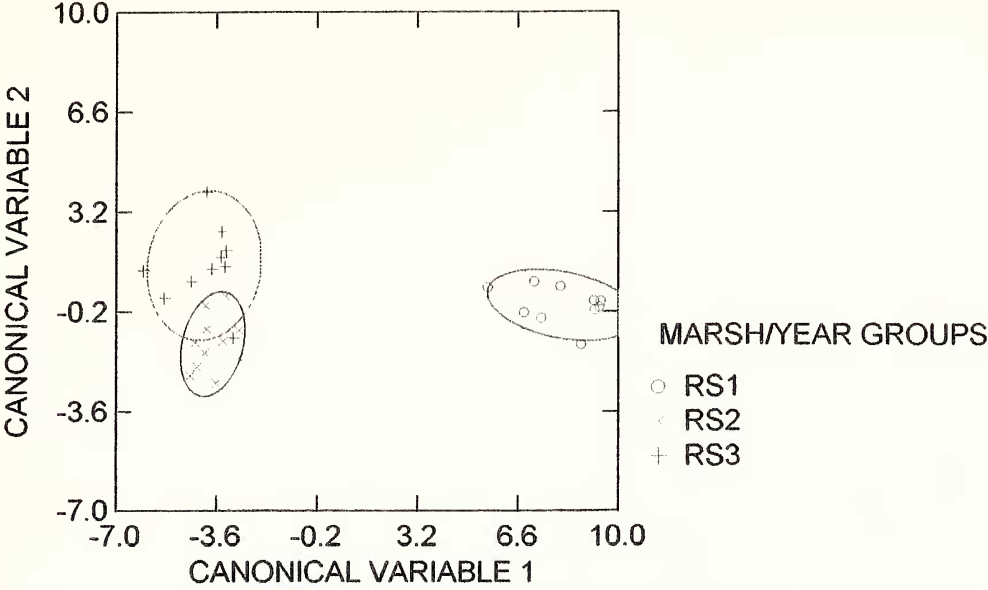


FIG. 3. Canonical scores plot for the reproductive success model of the discriminant function analysis. Soil moisture and nitrate + nitrite concentrations appeared to provide most of the separation between RS1 and RS2/RS3. Abiotic factors were also able to separate RS2 and RS3, although the separation appeared weaker.

was able to correctly predict or classify sampling locations 100 percent of the time (jackknifed classification matrix = 97 percent).

The reproductive success analysis was also successful at using nine of the biotic and abiotic variables to discriminate between the three groups suggested by multiple comparison results ( $F = 18.04$ ,  $n = 31$ ,  $P < 0.0001$ ; Fig. 3). Canonical scores of group means were (8.09, 0.03) for RS1, (-3.72, -1.29) for RS2, and (-4.00, 1.38) for RS3. The canonical discriminant function, which has two variables, accounted for 100 percent of the total dispersion in the data. The first canonical variable accounted for approximately 96 percent of the data dispersion. The canonical variables and a list of group means are provided in Table 2. As Figure 3 illustrates, most of the group separation comes from the first canonical variable, which appears to split RS1 (San Dieguito 1996) from the other marsh/years. The first canonical variable had strong loadings for nitrates + nitrites, soil moisture, phosphorous, ammonium, and organic matter. The second canonical variable involved separation of RS2 from RS3, although the degree of separation relative to RS1 appeared weaker. At least three of the sampling locations from RS2 appeared to associate more strongly with RS3, while one of the RS3 locations was grouped with RS2 (Fig. 3). The second canonical variable had strong loadings for phosphorous, magnesium, soil moisture, ammonium, and nitrates + nitrites. Using the canonical variables, the model was able to correctly classify sampling locations 100 percent of the time (jackknifed classification matrix = 100 percent).

The strong separation of marsh/year groups effected by soil moisture, phosphorous, cation exchange capacity, and calcium supports the premise that resources are the primary limiting factors of reproductive potential. Standardized canonical coefficients and group means for soil moisture, cation exchange capacity, and calcium concentrations point to a positive, perhaps even linear, relationship between resource factor and plant variable (Table 2—canonical variable).

The relationship between phosphorous concentrations and *L. glabrata* subsp. *coulteri* yield appears somewhat more complicated than that for soil moisture, cation exchange capacity, and calcium concentrations. Standardized coefficients suggest that elevated phosphorous concentrations may actually drive the canonical score toward RP1, which had a low yield. In contrast, group means show highest phosphorous concentrations in marsh/years with the highest reproductive potential. This disparity between group means and standardized coefficients for phosphorous also occurred in the reproductive success model.

As shown in Figure 3, resources also appear to play a role, if perhaps a more limited one, in reproductive success. As hypothesized earlier, the suite of factors influencing vegetative yield appeared to be slightly different from that affecting seed production, which may account for the difference in reproductive success observed between marsh/years with similarly sized individuals (San Dieguito Lagoon 1996 and San Dieguito Lagoon 1997). While soil moisture and phosphorous concentrations featured prominently in both analyses,



nitrogen concentrations (ammonium and nitrates + nitrites) appeared to have a larger effect on reproductive success than on reproductive potential. As was the case with phosphorous, standardized coefficients for nitrates + nitrites and ammonium suggest that elevated concentrations of inorganic nitrogen may actually drive canonical scores toward RS1 and a reduced reproductive yield, although group means for ammonium were marginally higher in RS3 than in either RS1 or RS2. Based on standardized coefficients and group means, only organic nitrogen sources such as organic matter appeared to contribute directly to enhanced seed production.

The evidence for resource limitation of seed production is somewhat weaker for the RS2 and RS3 groups. The reproductive success analysis did provide at least enough separation between RS2 and RS3 using canonical variable 2 to enable successful group differentiation and prediction. As with canonical variable 1 (Table 2), standardized coefficients for phosphorous in canonical variable 2 again appear to drive canonical scoring toward reduced yield, despite the fact that phosphorous concentrations were slightly higher in the group producing the most seeds (RS3). However, in contrast to canonical variable 1, inorganic nitrogen, along with soil moisture and magnesium, appeared to play a positive role in influencing reproductive yield. While the biotic and abiotic factors included in the analysis do enable successful separation between RS2 and RS3, the slight to moderate overlap between groups displayed graphically in Figure 3 suggest that, at some resource level, the number of seeds produced may be driven by other factors not included in this analysis, the most probable of which is pollen supply.

#### DISCUSSION

Soil moisture would seem an unlikely constraint in a salt marsh, but the high marsh represents a distinct ecotone in an aquatic environment. In general, high marsh species must contend with a complex series of hydrologic cycles: days or even weeks of flooding in the winter may be followed by months where the high marsh or marsh periphery is only inundated or saturated from subsurface flow during the highest high tides. The hydrologic complexity is compounded in managed lagoons, where the lagoon may be flooded deliberately to attract waterfowl or the tidal inlet may remain closed for most of the year even after winter storms elevate internal water levels. In several instances, water or moisture stress has been singled out as a primary factor limiting growth of species in the upper marsh zones (Boorman 1971; De Leeuw et al. 1990). Conversely, too much water or waterlogging can negatively affect species adapted to the typically well-drained soils of the high marsh or marsh periphery (Phleger 1971; Nestler 1977; Parrondo et

al. 1978; Cooper 1982; Seliskar 1985; Adams and Bate 1994).

Waterlogging may account for the anomalous results recorded in 1998, when survival (L. Parsons personal observation) and reproductive yield of the San Elijo Lagoon population plummeted and was significantly less than that of San Dieguito Lagoon. Nineteen ninety-eight was the one year during our study when rainfall was above average (178 percent of average during the months October–April; Table 1). During that year, back-up of run-off and creek flows kept water levels within the eastern area of the lagoon substantially elevated for weeks. In general, reproductive yield of this population was actually highest in the two years where rainfall was slightly below average—1997 (73 percent of average) and 1999 (67 percent of average). In below-average years, the current hydrologic management regime, in which the sluice gates are closed for waterfowl enhancement and outflow is provided through dips in a dike system, may actually enhance the population by artificially maintaining saturated soil conditions within the eastern portion of the lagoon. Conversely, the response of the San Dieguito Lagoon population to rainfall is more consistent with plants being limited by lack of water. Above-average rainfall during 1998 was directly associated with dramatic increases in vegetative and reproductive yield. The positive association between rainfall and yield, combined with the strong evidence of resource limitation in discriminant function analyses, suggests that, at San Dieguito Lagoon, rainfall both directly and indirectly boosts input and cycling of resources such as water and nutrients.

The importance of nutrient limitation in coastal salt marsh plant communities has been well documented (Tyler 1967; Pomeroy et al. 1969; Valiela and Teal 1974; DeLaune et al. 1979; Smart 1982; Long and Mason 1983; Mitsch and Gosselink 1986; Covin and Zedler 1988; Langis et al. 1991; Parsons and Zedler 1997; Boyer and Zedler 1988 and 1999). Our results generally show that higher yields are linked to higher nutrient concentrations. The seemingly negative relationship between phosphorous and inorganic nitrogen concentrations and plant yield observed in analyses could have resulted from some indirect effect of nutrient influx, such as greater competition with more abundant species for light, moisture, or nutrients (Bollens et al. 1998). However, neither total plant cover or cover of non-native species factored strongly into the discriminant function analyses. Based on group means showing elevated levels of phosphorous and, to some extent, ammonium in high yield plots (Table 2), it is more probable that these nutrients must interact with other resource variables in such a way that yield is maximized in areas with moderate concentrations of phosphorous and inorganic nitrogen. If such an interaction exists, our analyses were not sensitive enough to detect it, as no strong correla-

tion was evident between biotic and abiotic dependent or predictor variables (correlation <71 percent).

In general, plasticity in growth or reproduction in relation to rainfall and changes in soil moisture and nutrient input should be expected in annual plant species within Mediterranean climates, even in aquatic systems such as salt marshes. These opportunistic life forms must rely almost entirely on nature's largesse to propagate, survive, and succeed as they have none of the mechanisms (e.g., deep taproots, strongly developed mycorrhizal associations, waxy cuticle layer on leaves, etc.) that enable perennial plants to cope with drought and other climatic challenges. Several studies on salt marsh annuals, including an occurrence of *L. glabrata* subsp. *coulteri* at Carpinteria Marsh near Santa Barbara, California, have linked above average rainfall to increases in relative abundance (Allison 1992; Parsons and Zedler 1997) and density, distribution, and biomass (Callaway and Sabraw 1994). Terrestrial species are also strongly influenced by soil moisture (Reynolds et al. 1997; Center for Conservation Biology 1994), with yield for grassland members of *Lasthenia* such as *L. californica* optimized both during wet years and when growing in wet microsites (Hobbs and Mooney 1991, 1995). For perennial species, the effect of below average rainfall may be more subtle than for annuals, though no less significant, resulting in substantial reductions in seed set (Morgan 1999) and ultimately recruitment and population growth rates (Maschinski et al. 1997).

Plasticity in reproduction can be exacerbated by inter-annual variability in other types of "resources" such as pollen. While no information exists on the mating system of southern California coastal populations, in general, *L. glabrata* subsp. *coulteri* has been categorized as one of the 14 of 17 *Lasthenia* species that is self-incompatible (Ornduff 1966). Several species of insects such as bees, bee flies, flies, and beetles were observed visiting flowers, although what role these species have in effecting pollination of *L. glabrata* subsp. *coulteri* is unknown. Based on the species' presumed status as an entomophilous outcrosser, reproductive yield must depend to some degree on pollination success. As with their host species, pollinators, some of which are believed to nest in marshes or adjacent upland areas, can be affected by climatic variations and watershed disturbances, including flooding (Stephen et al. 1969).

Given the myriad of ecological interactions involved, it is not surprising that the factors governing reproductive potential and success of *L. glabrata* subsp. *coulteri* may prove complex both in terms of time and scale. A number of recent studies have supported the potential for spatial or temporal heterogeneity in resource and pollen limitations (McCall and Primack 1987; Zimmerman and Aide 1989; Campbell and Halama 1993; Lawrence 1993;

Parsons 1994; Parsons and Zedler 1997). Our study supports not only inter-annual heterogeneity in resource limitations, but possibly intra-annual heterogeneity, as well. For example, while reproductive potential and rainfall totals between October–March were similar for the 1996 and 1999 San Dieguito Lagoon populations, seed set was higher in 1999 than in 1996. A series of storms in early April 1999 may have eased resource constraints during the seed set period, allowing the sparse population of small plants to produce comparatively larger numbers of seed. In general, however, the complex hydrology of urbanized watersheds with dams, year-round urban run-off, and mouth closures would seemingly argue against a tight linkage between rainfall patterns and resource inputs and cycling.

## CONCLUSIONS

As we originally surmised, the *L. glabrata* subsp. *coulteri* population at San Dieguito Lagoon is not only smaller than the one at San Elijo Lagoon, but, based on trends in seed production, less stable, as well. For the most part, plants at San Dieguito Lagoon were smaller and produced less flowers and capitulescences and seed than those at San Elijo Lagoon. However, the nature of this relationship appears to be temporally variable and highly dependent on climatic conditions such as rainfall totals and distribution. In a year with above-average rainfall, yield of the San Dieguito Lagoon population was similar to and, in some ways, greater than that of the more stable one at San Elijo Lagoon. As rainfall is often linked directly and indirectly to inputs and cycling of resources such as water and nutrients, the strong association found between resources and reproductive potential and, to some extent, reproductive success is certainly not surprising, although the relationship was not always either simple or linear. Too much water actually appeared to decrease survival and reproductive yield of the 1998 San Elijo Lagoon population by inducing "waterlogging." In addition, some nutrients such as inorganic nitrogen and phosphorous may require higher levels of other resources such as soil moisture before exerting a positive effect on growth or reproduction of *L. glabrata* subsp. *coulteri*. When resources are sufficient, seed production appears to be limited by other "resources," the most probable of which is pollen supply.

The importance of the relationship between climatic conditions and population productivity assumes a deeper significance when considering the long-term viability of the small San Dieguito Lagoon population. Obviously, less seed will be produced in years when few plants are present or plant vigor is reduced. Still, even when the San Dieguito Lagoon population was relatively large and produced more seed per plant than the San Elijo Lagoon one, productivity of the San Dieguito Lagoon



population as a whole was still comparatively lower, because of the difference between marshes in population size. To some extent, the impact of consistently producing small numbers of seed could be offset if seed banks are long-lived and/or seed viability and germination rates are high. No research has been specifically conducted on seed bank longevity of *L. glabrata* subsp. *coulteri*, but studies on various *Lasthenia* species have documented long-lived seed banks (10 y; Vivrette 1999) and high germination rates in the field (25 to 69 percent; Thorp 1976) and laboratory (34 to 90 percent; Kingsbury et al. 1976; Callaway et al. 1990; Rajakaruna and Bohm 1999; Michael Wall personal communication, March 1999; Doug Gibson unpublished data). However, there are indications that germination or emergence from the seed bank for some *Lasthenia* species may be tightly regulated by the same climatic conditions (Vivrette 1999) that appear to negatively affect yield of *L. glabrata* subsp. *coulteri*, at least at San Dieguito Lagoon. Some evidence for this could be seen in the low number of plants present at San Dieguito Lagoon in 2000 (six plants; A. Thorpe personal communication), when rainfall during the primary germination period (October–January) totaled only 10.4 percent of average (San Diego NWS-Lindbergh; California Department of Water Resources, California Data Exchange Center). In drought years, then, both recruitment and individual yield could be reduced, thereby further diminishing productivity of the population as a whole.

Poor recruitment and yield in all but above-average rainfall years is of concern for populations in a region such as southern California, where above-average rainfall years are sporadic and often interspersed between lengthy periods of drought or below-average rainfall. In San Diego County, below-average rainfall occurs 60 percent of the time, while above-average rainfall occurs about 40 percent of the time (Elwany et al. 1998). There are suggestions that variability of this already extremely variable climate may be increasing due to global warming. Chronically low numbers of plants in average to below-average rainfall years can increase populations' susceptibility to genetic bottlenecks or extinction due to stochastic or disturbance-related events. Long-term viability of small populations such as San Dieguito Lagoon will probably depend on whether the species can germinate and reproduce successfully under average, as well as above-average, rainfall and climatic conditions. Future monitoring efforts should focus on assessing reproductive potential and success of this population under a variety of climatic and hydrologic conditions, as well as better defining pollinator relationships, breeding system, survivorship, seed bank dynamics, and field germination rates of *L. glabrata* subsp. *coulteri*.

#### IMPLICATIONS FOR MANAGEMENT AND RESTORATION

The information from this study will provide both preserve and restoration managers with some guidelines for future efforts to enhance or even reintroduce *L. glabrata* subsp. *coulteri* into salt marshes. Based on our results, *L. glabrata* subsp. *coulteri* grows best in marshes with moist, but not waterlogged, soils with low to moderate salinity, high cation exchange capacity, high percentage of organic matter, and moderate concentrations of phosphorous, calcium, and possibly ammonium. To ensure a high potential for project success, managers interested in conducting enhancement or reintroduction projects should carefully evaluate site conditions and hydrologic management regimes. While the goal of restoration and enhancement continues to revolve around creation of self-sustaining ecosystems, the reality is that many of our wetland ecosystems are now highly managed through tide or sluice gates, dikes, culverts, mechanical mouth breaching, and even deliberate floodings to attract waterfowl. If management cannot be avoided, it can perhaps be manipulated to provide benefits to species other than waterfowl. Indeed, the high yield recorded at San Elijo Lagoon in years with below-average rainfall may result in part from artificially elevated soil moisture conditions created by back-up of run-off and creek flows when sluice gates are closed during the winter.

While, as a science, restoration ecology has moved away from a single-species management approach, there is still a strong need for single-species-focused research. Without carefully understanding the biotic and abiotic relationships that drive individual species within an ecosystem, we might be tempted to make gross generalizations about the habitat linkages without ever really grasping the framework of those linkages. For example, what functions of the high marsh are particularly important for *L. glabrata* subsp. *coulteri*, and how do these needs complement or detract from those of other species inhabiting this fragile ecotone, such as *Cordylanthus maritimus* Benth. subsp. *maritimus* or *Panoquina errans* (wandering skipper butterfly)? Directed research on each of these species provides the pieces for the larger ecosystem puzzle. It is up to restoration and preserve managers to put the puzzle together in a manner that will maximize benefits for as many species as possible, as well as the ecosystem as a whole.

#### ACKNOWLEDGMENTS

The authors would like to thank Doug Gibson, John Boland, Troy Kelly, and Roger Briggs for their assistance with this project. We also thank Bonnie Peterson for her contribution to data collection. The comments of Kathy Boyer, Jessica Martini-Lamb, and two reviewers improved this manuscript.



LITERATURE CITED

ADAMS, J. B. AND G. C. BATE. 1994. The effect of salinity and inundation on the estuarine macrophyte *Sarcocornia perennis* (Mill.) A. J. Scott. *Aquatic Botany* 47:341-348.

ALLISON, S. K. 1992. The influence of rainfall variability on the species composition of a northern California salt marsh plant assemblage. *Vegetatio* 101:145-160.

BARRETT, S. C. H. AND J. R. KOHN. 1991. Genetic and evolutionary consequences of small population size in plants: implications for conservation, Pp. 3-30. in D. A. Falk, and K. E. Holsinger (eds.). *Genetics and conservation of rare plants*. Oxford University Press, New York, N.Y.

BOLLENS, U., S. GUSEWELL AND F. KLOTZLI. 1998. On the relative importance of nutrient availability and water level for the biodiversity of wet meadows. *Bulletin of the Geobotanical Institute ETH* 64(0):91-101.

BOORMAN, L. A. 1971. Studies in salt marsh ecology with special reference to the genus *Limonium*. *Journal of Ecology* 59:103-120.

BOYER, K. E. AND J. B. ZEDLER. 1998. Effects of nitrogen additions on the vertical structure of a constructed cordgrass marsh. *Ecological Applications* 8(3):692-705.

BOYER, K. E. AND J. B. ZEDLER. 1999. Nitrogen addition could shift plant community composition in a restored California salt marsh. *Restoration Ecology* 7(1):74-85.

CALIFORNIA WETLANDS INFORMATION SYSTEM. 1996. California Environmental Research Exchange System (CERES). California Resources Agency, Sacramento, CA. Electronic communication (web site).

CALLAWAY, R. M., S. JONES, W. R. FERREN, JR. AND A. PARIKH. 1990. Ecology of a mediterranean-climate estuarine wetland at Carpinteria, California: plant distributions and soil salinity in the upper marsh. *Canadian Journal of Botany* 68:1139-1146.

CALLAWAY, R. M. AND C. S. SABRAW. 1994. Effects of variable precipitation on the structure and diversity of a California salt marsh community. *Journal of Vegetation Science* 5:433-438.

CAMPBELL, D. R. AND K. J. HALAMA. 1993. Resource and pollen limitations in seed production in a natural plant population. *Ecology* 74(4):1043-1051.

CENTER FOR CONSERVATION BIOLOGY. 1994. Conservation of the palmate-bracted bird's beak, *Cordylanthus palmatus*. Stanford University, Stanford, CA.

CHARLESWORTH, D. AND B. CHARLESWORTH. 1987. Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* 18:237-268.

COOPER, A. 1982. The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. *New Phytologist* 90:263-275.

COVIN, B. AND J. B. ZEDLER. 1988. Nitrogen effects on *Spartina foliosa* and *Salicornia virginica* in the salt marsh at Tijuana Estuary, Calif. *Wetlands* 8:51-65.

DAVY, A. J. AND R. L. JEFFERIES. 1981. Approaches to the monitoring of rare plant populations, Pp. 219-232. in H. Synge, (ed.). *The biological aspects of rare plant conservation*. John Wiley & Sons, London, United Kingdom.

DELAUNE, R. D., R. J. BURESH AND W. H. PATRICK, JR. 1979. Relationship of soil properties to standing crop biomass of *Spartina alterniflora* in a Louisiana marsh. *Estuarine Coastal Marine Science* 8:477-487.

DE LEEUW, J., H. OLFF AND J. P. BAKKER. 1990. Year-to-year variation in peak above-ground biomass of six salt marsh angiosperm communities as related to rainfall deficit and inundation frequency. *Aquatic Botany* 36:139-151.

ELWANY, M. H. S., R. E. FLICK AND S. ADJAZ. 1998. Opening and closure of a marginal southern California lagoon inlet. *Estuaries* 21(2):246-254.

ELWANY, M. H. S. 1999. Professor. Center for Coastal Studies, Scripps Institution of Oceanography, La Jolla, CA. Unpublished data.

GARDNER, W. H. 1986. Water content in *Methods of Soil Analysis*, part 1: physical and mineralogical methods, 2nd ed. American Society of Agronomy—Soil Science Society of America. Madison, WI.

HAMRICK, J. L., Y. B. LINHART AND J. B. MITTON. 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. *Annual Review of Ecology and Systematics* 10:173-200.

HARPER, J. L. 1977. *Population biology of plants*. Academic Press, London, United Kingdom.

HEDRICK, P. W. 1983. *Genetics of populations*. Science Books International. Boston, MA.

HICKMAN, J. C. 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley.

KINGSBURY, R. W., A. RADLOW, P. J. MUDIE, J. RUTHERFORD AND R. RADLOW. 1976. Salt stress responses in *Lasthenia glabrata*, a winter annual composite endemic to saline soils. *Canadian Journal of Botany* 54: 1377-1385.

LANGIS, R., M. ZALEJKO AND J. B. ZEDLER. 1991. Nitrogen assessments in a constructed and natural salt marsh of San Diego Bay. *Ecological Applications* 1:40-51.

LAWRENCE, W. S. 1993. Resource and pollen limitation: plant size-dependent reproductive patterns in *Physalis longifolia*. *American Naturalist* 141(2):296-313.

LEDIG, F. T. 1986. Heterozygosity, heterosis, and fitness in outbreeding plants, p. 77-104. in M. E. Soule, (ed.). *Conservation biology: the science of scarcity and diversity*. Sinauer Press, Sunderland, MA.

LONG, S. P. AND C. F. MASON. 1983. *Saltmarsh ecology*. Cambridge University Press, Cambridge, United Kingdom.

MASCHINSKI, J., R. FRYE AND S. RUTMAN. 1997. Demography and population viability of an endangered plant species before and after protection from trampling. *Conservation Biology* 11(4):990-999.

MCCALL, C. AND R. B. PRIMACK. 1987. Resources limit the fecundity of three woodland herbs. *Oecologia* 71: 431-435.

MEC ANALYTICAL SYSTEMS, INC. 1993. San Dieguito Lagoon restoration project biological baseline study, March 1992-May 1993, Vol. 1, 2nd ed. Draft technical memorandum. Prepared for Southern California Edison, Rosemead, CA.

MENGES, E. S. 1986. Predicting the future of rare plant populations: demographic monitoring and modeling. *Natural Areas Journal* 6(3):13-25.

MENGES, E. S. AND D. R. GORDON. 1996. Three levels of monitoring intensity for rare plant species. *Natural Areas Journal* 16(3):227-237.

MITSCH, W. J. AND J. G. GOSSELINK. 1986. *Wetlands*. Van Nostrand Reinhold Company, New York, NY.

MORGAN, J. W. 1999. Effects of population size on seed production and germinability in an endangered, frag-

- mented grassland plant. *Conservation Biology* 13(2): 266–273.
- NATURAL DIVERSITY DATA BASE (NDDDB). 1998. California Department of Fish and Game. Sacramento, CA.
- NEI, M. 1989. *Molecular population genetics and evolution*. Elsevier, New York, N.Y.
- NESTLER, J. 1977. Interstitial salinity as a cause of ecophenic variation in *Spartina alterniflora*. *Estuarine and Coastal Marine Science* 5:707–714.
- ORNDUFF, R. 1966. A biosystematic survey of the goldfield genus *Lasthenia* (Compositae:Helenieae). *University of California Publications in Botany* 40:1–92.
- PARRONDO, R. T., J. G. GOSSELINK AND C. S. HOPKINSON. 1978. Effects of salinity and drainage on the growth of three salt marsh grasses. *Botanical Gazette* 139(1): 102–107.
- PARSONS, L. S. 1994. Re-establishment of salt marsh bird's beak at Sweetwater Marsh: factors affecting reproductive success. Master's Thesis, San Diego State University, San Diego, CA.
- PARSONS, L. S. AND J. B. ZEDLER. 1997. Factors affecting reestablishment of an endangered annual plant at a California salt marsh. *Ecological Applications* 7(1): 253–267.
- PAVLIC, B. M. 1994. Demographic monitoring and the recovery of endangered plants. Pp. 322–350. *in* M. L. Bowles, and C. J. Whelan (eds.). *Restoration of endangered species: conceptual issues, planning and implementation*. Cambridge University Press, Cambridge, United Kingdom.
- PHLEGER, C. F. 1971. Effect of salinity on growth of salt marsh grass. *Ecology* 52:908–911.
- POMEROY, L. R., R. E. JOHANNES, E. P. ODUM AND B. ROFFMAN. 1969. The phosphorous and zinc cycles and productivity of a salt marsh. Pp. 412–419. *in* D. J. Nelson, and F. C. Evans (eds.). *Proc. 2nd Natural Symposium on Radioecology*.
- POWELL, A. H. AND G. V. N. POWELL. 1987. Population dynamics of male euglossine bees in Amazonian forest fragments. *Biotropica* 19:176–179.
- PURER, E. A. 1942. Plant ecology of the coastal salt marshlands of San Diego County, California. *Ecological Monographs* 12(1):83–111.
- RAJAKARUNA, N. AND B. A. BOHM. 1999. The edaphic factor and patterns of variation in *Lasthenia californica* (Asteraceae). *American Journal of Botany* 86(11): 1576–1596.
- REYNOLDS, H. L., B. A. HUNGATE, F. S. CHAPIN, III AND C. M. D'ANTONIO. 1997. Soil heterogeneity and plant competition in an annual grassland. *Ecology* 78(7): 2076–2090.
- SAN DIEGO COUNTY DEPARTMENT OF PARKS, AND RECREATION. UNPUBLISHED DATA. Recording of date of mouth opening, duration of opening, and type of opening (artificial vs. natural). San Diego, CA.
- SCHEMSKE, D. W., B. C. HUSBAND, M. H. RUCKELSHAUS, C. GOODWILLIE, I. M. PARKER, AND J. G. BISHOP. 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* 75(3):584–606.
- SEA SCIENCE SERVICES, AND PACIFIC SOUTHWEST BIOLOGICAL SERVICES, INC. 1980. Report on environmental baseline studies for the San Dieguito Lagoon Enhancement Plan, Del Mar, California. Prepared for the Department of Planning and Community Development, City of Del Mar and the State of California Coastal Conservancy.
- SELISKAR, D. M. 1985. Morphometric variations in five tidal marsh halophytes along environmental gradients. *American Journal of Botany* 72(9):1340–1352.
- SHAFFER, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131–134.
- SKINNER, M. W. AND B. M. PAVLIK. 1994. Inventory of rare and endangered vascular plants of California. California Native Plant Society, Sacramento, CA.
- SMART, R. M. 1982. Distribution and environmental control of productivity and growth form of *Spartina alterniflora*. *in* D. N. Sen, and K. S. Rajpurokit (eds.). *Contributions to the ecology of halophytes*. Dr. Junk, The Hague, The Netherlands.
- SOKAL, R. R. AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman and Company, New York, N.Y.
- STEPHEN, W. P., G. E. BOHART AND P. F. TORCHIO. 1969. *The biology and external morphology of bees*. Agricultural Experiment Station, Oregon State University, Corvallis, OR.
- THORP, R. W. 1976. Insect pollination of vernal pool flowers. Pp. 36–40. *in* S. Jain (ed.), *Vernal pools, their ecology, and conservation*. Institute of Ecology Publication No. 9. University of California-Davis, Davis, CA.
- TYLER, G. 1967. On the effect of phosphorous and nitrogen, supplied to Baltic shore-meadow vegetation. *Botaniska Notiser* 120:433–447.
- VALIELA, I. AND J. M. TEAL. 1974. Nutrient limitation in salt marsh vegetation. Pp. 547–563. *in* R. J. Reinhold and W. H. Queen (eds.). *Ecology of halophytes*. Academic Press, New York, NY.
- VIVRETTE, N. 1999. Coastal bluff vegetation change over 25 years on Santa Cruz Island *in* Fifth California Islands Symposium: schedule of symposium proceedings and events and presentation and poster abstracts. March 29–April 1, 1999.
- WALL, M. 1999. Seed curator. Rancho Santa Ana Botanic Garden at Claremont, Claremont, CA. Personal communication.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.
- ZIMMERMAN, J. K. AND T. M. AIDE. 1989. Patterns of fruit production in a neotropical orchid: pollinators vs. resource limitation. *American Journal of Botany* 76(1): 67–73.